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 of Mothers and Infants in Semi-Free
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Variability in Weaning-Related Behaviors of Mothers and
Infants in Semi-Free Ranging Japanese Macaques (*Macaca*
fuscata)



by

Nancy E. Collinge

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH
IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE
OF Master of Arts

Department of Anthropology

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Fall 1985

THE UNIVERSITY OF ALBERTA
FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled Variability in Weaning-Related Behaviors of Mothers and Infants in Semi-Free Ranging Japanese Macaques (*Macaca fuscata*) submitted by Nancy E. Collinge in partial fulfilment of the requirements for the degree of Master of Arts.

Abstract

The purpose of this research was to investigate variability in the weaning-related behaviors of primate mothers and their infants; to attempt to define factors contributing to this variability; and to provide some insights into the dynamics of the mother-infant bond. The study was conducted on Japanese macaques (*Macaca fuscata*) at the Arashiyama West Primate Center near Dilley, Texas. The analysis was based on 344 hours of focal animal data gathered during the breeding season of 1983 on 18 mothers with 4 - 8 month old infants.

The marked level of variability in maternal weaning-related behaviors was found to be unrelated to traditional explanatory factors, such as the rank, parity and age of the mother, and the sex and number of immature siblings of the infant. It is possible that the effects of maternal rank and parity, and the sex of the infant on the behaviors of the mothers, often cited in the literature, occurred when the infants were younger than 4 months of age.

There was little variability in the weaning-related behaviors of the infants except in the rates of distress reactions and attempts to gain nipple contact, which were the only behaviors which were correlated with any maternal behaviors at a significant level. The infants exhibited distress and sought the nipple more, as the rates of maternal rejection increased.

Eleven of the subject females began their estrous cycles during the study. The estrous state of the mother was the one factor which could be used to predict variations in the rejective behaviors of the mothers and the infants' distress reactions. The frequency of maternal rejection did not escalate as the infants grew older, however there was a significant increase in the rate of rejections during the estrous sessions of those females who cycled. Only the infants of the females who cycled exhibited a higher level of distress reactions as they grew older. Although the higher ranking, older and more experienced mothers appeared to be the focus of a higher rate of infant advances in the overall sample, these results were significantly more evident in the females who cycled.

Trivers has provided a sociobiological explanation for such results, arguing that the mother-infant conflict over weaning is a function of divergent selective pressures on the mothers and their current infants, which will be particularly evident when the females are in estrus and motivated to mate.

The results of this study suggest that the variability in the weaning-related behaviors of the infants in the present study was more a function of the variability in the maternal behaviors and the estrous state of the mothers, than a function of their own behavioral diversity.

The fact that the infants were spending over half their time within 1 meter of their mothers reinforced the general

impression from field observations, that the infants had not yet achieved a great deal of independence.

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I. Introduction

The State of the Field With Respect to Primate Weaning

The mother-infant bond in most primate species has generally been recognized as the most important relationship of an individual's life, not only because it is the first bond ever formed but also because of its intense nature and the fact that it may form the pattern for all future bonds (Jensen et al. 1967). Life history patterns influence the intensity and the socializing potential of the mother-infant relationship. Because a primate mother usually bears a single infant which is dependent upon her for nourishment, comfort protection and transportation and the period of dependency is prolonged, the mother is recognized as the critical socializing agent (Poirier 1972). Thus, it is not surprising that there have been a number of studies concerning the mother-infant relationship in non-human primates that trace the socialization and the development of the infant from birth, over periods ranging from 30 weeks to two and one-half years. Much of the literature deals with factors affecting maternal behaviors and infant development, such as deprivation of the mother, absence or presence of peers or a restricted versus a stimulating environment.

Harlow et al. (1963:257) have suggested that 3 stages of maternal behavior can be defined in the ontogeny and the development of independence in young rhesus monkeys (*Macaca mulatta*):

1. Maternal attachment and protection
2. Maternal ambivalence
3. Maternal separation and rejection.

This scheme is an oversimplification of a complex process but provides a useful way to look at the temporal sequence of behaviors and interactions (Rosenblum 1971).

Weaning is the process of loosening the mother-infant bond, resulting in the independence of the young. The onset of weaning coincides with the second stage, maternal ambivalence, and continues through Stage 3. Any operational definition of weaning must stress the fact that weaning is a gradual process and that there are several aspects involved: nutrition, accustoming the young animal to the loss of its mother's milk, and the severing of psychological and emotional dependence on the mother (Altmann 1980; Martin 1984). Nutritional weaning can be accomplished when the infant is able to sustain itself, but the comfort and emotional security gained from suckling and physical contact with the mother may still continue to be necessary (Galef 1981; Martin 1984).

Weaning appears to be a traumatic time for most young non-human primates, as they often react to maternal rejections with tantrums and vocalizations in their efforts to regain physical contact (Altmann 1980; Jay 1963; Nicolson 1982). Harlow et al (1963), in a 21 month study of young rhesus macaques (*Macaca mulatta*), never did see a true physical separation of mothers and their infants. They

suggested that in the feral state, although physical separation may take place at the appearance of the next infant, psychological separation is not complete. This is also plausible in the case of Japanese macaques (*Macaca fuscata*), where female offspring often stay close to their mothers for life (Fedigan 1982; Harlow et al 1963).

Despite the fact that the acquisition of independence would seem to be a major milestone in the behavioral development of an individual, weaning per se has been generally neglected by primatologists and treated as just one phase in the socialization process. Poirier (1972:14) states:

one aspect of the non-human primate maternal-infant behavioral system that has been largely ignored except on the gross level, is the weaning process

Almost a decade later Gubernick and Klopfer (1981:x) remark that

The process of weaning has also received comparatively little analysis or theoretical treatment despite its importance in the transition of an infant from a dependent to an independent existence.

Martin (1984:1257), in a recent article, is also of the opinion that, although it represents a major transition in the life of the young, "weaning is a poorly understood and neglected issue". Since 1981, with a few notable exceptions,¹ weaning in non-human primates has not been a major issue in mother-infant studies. Clearly, despite the

¹ J.R. Horvath and H.C. Kraemer (1982). Behavioral Changes During Weaning in Captive Chimpanzees
N.A. Nicolson (1982). Weaning and the Development of Independence in Olive Baboons.

recognized importance of the weaning process, weaning-related studies have not gathered a great deal of momentum.

A. Research Question

A survey of the literature describing the life-ways of different species of non-human primate as well as studies dealing primarily with mother-infant relationships, indicates that there is a great deal of variation in maternal behavior between and within species. For example, North Indian Langurs (*Presbytis entellus*) females are among the most permissive mothers, allowing other females to handle and carry away new-born infants. Weaning begins early, at about 7 weeks, and is complete after a year (Jay 1963). In contrast, female baboons (*Papio sp.*) will not allow other members of the social group access to their new-born, although males and females exhibit great interest in their infants. Weaning in baboons begins abruptly when the infant is about 6 to 7 months of age and is complete in a year, after which the young can rely on adult males for protection (Altmann 1980; DeVore 1963). Vervet infants (*Cercopithecus aethiops*), compared to other Cercopithecine young such as macaques and baboons, are relatively precocial. They cling ventrally for a shorter time and are weaned earlier than other members of the family *Cercopithecidae* (Struhsaker 1971).

There are striking differences in the maternal behavior of females of closely related species such as bonnet (*Macaca radiata*) and pigtail macaques (*Macaca nemestrina*). Female pigtail macaques with new-born infants appear reluctant to interact socially with other females and are extremely protective with their young. Bonnet macaque mothers stay in close contact with other females and frequently allow them easy access to their new-born. They retrieve and protect their infants less, begin the weaning process earlier, but wean with much lower intensity than the pigtail mothers (Rosenblum and Kaufman 1967).

Some physical, social and environmental factors that are generally thought to contribute to the variability in maternal behavior between species are:

1. Group social structure (the availability of peers and adults with whom to interact)
2. Environmental adaptations (the degree of arboreality or terrestriality)
3. Environmental conditions (captive vs wild; resource availability)
4. Individual differences in infants (precocity, rate of maturation, presence of neo-natal coat)
5. Endocrinal differences in the mothers (birth spacing, gestation period, onset of estrus).

The literature suggests that although the actual progression of the weaning process from maternal ambivalence to serious rejection is similar for all non-human primate

species, there is wide variation in the onset, duration and intensity of weaning likely due to a combination of the above factors (Nash and Wheeler 1982).

It is generally agreed that a great deal of variation also exists in the weaning process and weaning-related behaviors of mothers and infants of the same species. Researchers have speculated on the reasons for this variation. Laboratory research has been conducted by Harlow et al (1963), Hinde (1974), Jensen et al (1967), Rosenblum (1971) and others, comparing maternal behaviors in the same species under deprived and enriched laboratory conditions. Horvat and Kraemer (1982) reported on the behavioral differences observed during the weaning of young chimpanzees in the wild and in captivity. Although the existence of intraspecific variability in the weaning behaviors of non-human primates living under the same conditions is frequently mentioned, there are few studies which define the degree of variability. This type of behavioral variation and its causes is the research question addressed in this thesis.

A review of the studies that have analysed the factors affecting the mother-infant relationship (such as the rank, age and parity of the mother and the age and sex of the infant), has yielded results that are "undramatic and conflicting" (Berman 1984:19). Berman (1984) suggests that this inconsistency is likely a function of the complexity of the mother-infant relationship, problems inherent in

statistical tests on small populations and the effect of different social and physical environments. Since it is difficult to avoid the first two problems in primatological research on mothers and their infants, a more practical strategy would be to discuss each species separately, recognizing the effects of the environment. Then, perhaps some general statements could be made applying to all primates.

B. Objectives

The primary purpose of the following study is to investigate the degree of variability in the weaning-related behaviors of mother and infant Japanese macaques (*Macaca fuscata*) and to attempt to determine if the variability is related to:

1. Sociological factors such as the rank, age, parity of the mother, number of immature offspring, and the sex of the infant
2. Ontogenetic or developmental factors such as the increasing age of the infant over the duration of the study
3. Ultimate or evolutionary factors which refer to a sociobiological explanation for the mother-infant conflict over weaning.

A secondary purpose is to use the results to make general statements about the dynamics of the mother-infant relationship in Japanese macaques (*Macaca fuscata*) during

weaning.

1. The Investigation of Variability in Weaning-Related Behaviors

a. Sociological Factors

The importance of sociological factors associated with the wide variation in mother-infant relationships in non-human primates has been investigated quite extensively since the mid 1960's in the laboratory and to a lesser extent in the field (Berman 1984). Although weaning per se has not been the major issue, the weaning period is included within the time-frame of these studies. As previously mentioned, the conflicting results of these studies provide little firm evidence regarding the definition of the factors which act on the mother-infant relationship overall and during the weaning process.

Rank of The Mother

The effect of maternal rank in infant rearing has been widely discussed in species which have a well defined female dominance hierarchy, such as Japanese macaques and baboons (Nash and Wheeler 1982). It has been observed that high ranking females are the recipients of less aggression than those of lower rank and consequently are more relaxed and confident in their relationships with their infants (Altmann 1980; DeVore 1963). However the rank of the mother has

proved to be the most inconsistent of all the traditional variables expected to affect the mother-infant relationship (Nash and Wheeler 1982). The research results vary widely, even between studies on the same species.

Altmann (1980) (baboons), DeVore (1963) (baboons), and White and Hinde (1974) (Rhesus macaques) report that infants of high ranking mothers are rejected more and spend more time away from their mothers than infants of medium and low ranking mothers. Gouzoules (1980) (Japanese macaques) and Kaufman and Rosenblum (1972) (rhesus macaques) found that infants of high ranking mothers are rejected less and spend more time with their mothers than other infants. Little marked difference in maternal behaviors was reported between mothers of different ranks by Berman (1984) (rhesus macaques) and Nicolson (1982) (baboons).

Parity

Berman (1984:19) states that:

most researchers agree that socially reared primipares or primipares that have at least had the opportunity to observe maternal care earlier in life, provide adequate care to infants. However they disagree about the extent to which mother-infant relationships of primiparous and multiparous mothers differ within the adequate range.

Some researchers have found that primiparous rhesus mothers are more anxious and protective and less rejecting than multiparous mothers (Hinde and Spencer Booth 1967; Kaufmann 1966; Mitchell and Stevens 1969). Nicolson (1982) reported that young baboon mothers begin rejecting their infants

earlier than the other mothers, while others have found no real differences in maternal behaviors related to parity (Berman 1984; Gouzoules 1980; White and Hinde 1975).

Age of the Mother

Trivers (1974) suggests that older mothers should be more willing to invest in their young because their own reproductive "value" is less than that of younger females. Older females have fewer reproductive years left thus their parental investment would be less detrimental to their future reproductive success. This could result in older mothers being more tolerant and less rejective of their current infants. This has been found to be the case generally in baboons at Gombe and Gilgil (Nicolson 1982) and in Japanese macaques in South Texas (Gouzoules 1980). However Berman (1984), in her research on wild rhesus monkeys at Cayo Santiago, found that older mothers rejected their infants more and spent more time at a distance from them than younger mothers.

Number of Immature Offspring

Berman (1984), Hinde and Spencer-Booth (1967) and Gouzoules (1980), in their studies of mother-infant relationships of macaques, found that females with more immature offspring were more rejecting and more encouraging of independence in their young.

Sex of the Infant

In several studies of captive rhesus macaques, male infants spent more time off their mothers and were rejected more after the first 3 months of life than female infants (Hinde and Spencer-Booth 1967; Jensen et al 1967; White and Hinde 1974). Altmann (1980), Berman (1984) and Gouzoules (1980) found insignificant differences related to the sex of the infant during weaning, while Nicolson (1982) found a difference only in the duration of dorsal carrying in olive baboons, which was shorter for male infants.

This field study attempts to test the effect of these traditional sociological factors on the weaning-related behaviors of semi free-ranging Japanese macaque (*Macaca fuscata*) mothers and infants.

b. Ontogenetic Factors

Results from studies on captive rhesus macaques indicate that maternal rejection reaches a minor peak from 23 to 24 weeks after birth (Hinde and Spencer Booth 1967), while in wild Japanese macaques there is a general intensification of weaning from 21 to 36 weeks after birth (Ehardt and Blount 1984). Berman (1984:23), in her 30 week field study of rhesus macaques, found that:

in general, interindividual differences in measures of mother-infant interactions remained constant from one age period to the next.

Since the infants in the present study range from 4 to 8

months of age when other studies show a levelling in the rate of maternal rejections, there may be few age-related differences in this area.

Field studies which address the mother-infant relationship during the weaning period report a gradual decrease in the duration of time the infants spend in physical contact and close to their mothers (Altmann 1980; Berman 1978; Nicolson 1982; Struhsaker 1961). The effect of the advancing age of the infants over the duration of the study on the weaning-related behaviors of the mothers and their infants and the mother-infant relationship in general will be tested.

c. Ultimate or Evolutionary Factors

Trivers (1974) has interpreted the weaning process through a sociobiological theory in which the parent-infant conflict could be used to explain the weaning behaviors of the mothers and the reactions of the infant. The costs of parental energy spent in nourishing, protecting, and caring for the young are weighed against the benefits, in terms of insuring their survival.

This theory stresses the active role played by the infant as well as the mother in the weaning process. Trivers suggests that the nature and course of parental behaviors could be predicted by viewing them as a function of the costs to the parent's reproductive success and the benefits to the survival of the current infant.

The mother is related equally to all her offspring and will be concerned with her ability to reproduce in the future as well as with the survival of her infant. The infant is totally related to itself and only partially related to its siblings and half-siblings and will be selected to seek more maternal care than the mother is selected to provide (Altmann 1980, Nash 1982). The mother-infant conflict over weaning, which to many appears to be an inefficient and counter-productive natural phenomenon, could be generated by this genetically-determined tug-of-war (Trivers 1974; Altmann 1980).

Galef (1981:212) suggests that a change is needed in the consideration of selective pressures responsible for the "apparent complementarity" between the course of maternal behaviors and the changing requirements of the young. He argues, as does Trivers (1974), that the infant is not the passive, inept partner in the mother-infant relationship and that the dependent young act "so as to maximize net energy gain within the constraints imposed by the dam's limited willingness to invest in them" (Galef:214). Each stage in the mother-infant relationship could be seen as a series of ecological niches, determined by the degree of utilization of the mother as a resource base, with each stage functionally complete. Galef (1981) likens the mother-infant relationship to a host-parasite relationship, the young mammal at each stage of development being analagous to a

type of parasite. For example, the pre-natal infant is likened to an endoparasite, which is internal to the host, the newborn to an obligate parasite, which is completely dependent on the host and later as a facultative parasite, which is partially dependent on the host. Each type of parasite is adapted to survive in the environment provided by the host. He sees the maturing mammal as changing behaviorally in order to adapt to each stage of its development or ecological niche, rather than progressing from dependence to independence (Galef 1981).

In the case of the weaning process, the estrous state of the mother could be viewed as creating a new ecological niche to which the infant must adapt by altering its behavior. It could be predicted that this conflict of interest should intensify during mating season, when the mother is predisposed to mate and produce further offspring.

Not all researchers, particularly Altmann (1980), credit the mother-infant conflict over weaning to sociobiological pressures. However, field studies investigating the ontogeny of infants and mother-infant relationships in non-human primates describe heightened levels of maternal rejection when the females resumed their estrous cycles (DeVore 1963; Horvat and Kraemer 1982; Jay 1963; Nash 1978; Ransom and Rowell 1972).

The present research could provide at least a partial assessment of Trivers' (1974) theory by comparing the weaning-related behaviors of mothers and their infants in

estrous and non-estrous periods. Variations in the behaviors of the infants between estrous and non-estrous sessions could also be used to test Galef's theoretical position.

2. Dynamics of the Mother-Infant Interaction

a. Infant Reactions to Maternal Rejection

There are 2 distinct types of infant reactions to maternal rejections described in the literature, distress reactions and attachment seeking behaviors.

(1) Distress Reactions

Although laboratory studies rarely mention the distress reactions of the infant, field studies of different species of non-human primates acknowledge vocalizations and tantrums as signs of distress associated with maternal weaning behaviors (Altmann 1980; Clark 1977; Jay 1973; Nicolson 1982; Poirier 1968). Altmann (1980) found that maternal punishing behaviors, in baboons such as bites and hits, were often followed by distress vocalizations and, less frequently, by tantrums. However, during the weaning period, the vocalizations occurred very often without any obvious rejection on the part of the mother. This could be an indication of the subtlety of maternal activities; their rejective behaviors sometimes being difficult to detect (Altmann 1980).

Nicolson (1982) differentiated between mild and severe rejections and states that in infant olive baboons, the "infant distress was associated with the severity of the mother-infant conflict" (Nicolson 1982:117). She found that severe maternal rejections, such as hitting, biting and pinning to the ground were positively related to infant distress reactions (Nicolson 1982).

(2) Attachment Behaviors

Harlow et al (1963), Hinde (1974), Kaufman (1974) and Rosenblum (1974), all of whom conducted laboratory research on the mother-infant relationship in various species of macaques, have reported that maternal rejections appear to increase the infant's desire for attachment and contact comfort. Field studies on other species have reported similar tendencies (Clark 1977; Poirier 1965). Thus, although it is generally acknowledged that maternal rejection plays an important part in the acquisition of independence of the young, at least temporarily, the aggression of the mother seems to have the opposite effect. Kaufman (1974:50) states

Within limits, then, [maternal] rejection generally leads to an increase in dependency behavior.

He explains the adaptive significance of this reaction of the infant by emphasizing the survival value of clinging when confronted with a negative stimulus, even if the stimulus is coming from a usual source of comfort.

The data from the present study could be used to (a) determine if the positive correlation between maternal rejection and infant attachment behaviors and durations found previously in the laboratory studies of rhesus, bonnet and pigtail macaques exists also in semi free-ranging Japanese macaques, and (b) test the relationship of infant distress reactions to maternal rejections.

b. Mother versus Infant. Their Respective Roles in the Maintenance of Proximity

Most studies of the mother-infant relationship in non-human primate indicate that, from the onset of weaning, the infants are the main agents in regulating the degree of proximity to their mothers (Berman 1984; Hinde 1974; Murray and Murdoch 1977; Nicolson 1982). However, the question of whether this initiative on the part of the infant is actually a function of the mother's rejection and reduced tendencies to approach her infant (Berman 1984) or a function of the infant's curiosity and social and physical mobility (Kaufman 1966) has never been resolved. In a complex interactive relationship, causal agencies are often difficult to establish. Both members of the mother-infant dyad are contributing to the status quo in some degree; the question is to what degree? McKenna (1979) argues that it is non-productive to try to determine which member of the pair is responsible for the overall situation. Researchers have argued both ways, using their own results to defend their

respective positions. Hansen (1966) in particular, emphasizes the active part played by the mother in determining the degree of independence of her young. He recognizes that it is often difficult to differentiate the role each plays in the course of mother-infant interactions and so bases his assumptions on the fact that infant rhesus monkeys leave their real mothers, who have been rejective, more frequently and earlier than infants with inanimate surrogate mothers. Hinde (1974) concurred that the mother provides the major impetus in determining the degree of proximity of the infant to its mother based on a positive correlation of maternal rejections and the time the infant was away from its mother.

Kaufman (1974), who conducted research on pigtail and bonnet macaques, argues that maternal rejection is an important factor in the maintenance of proximity. However he found that the effects of rejection vary over time and that other factors, such as the development of the infant's social and motor skills, were of significant importance in the degree of infant independence. He based his assumptions on the fact that, although pigtail mothers were more rejective than bonnet mothers, at the end of the first year the pigtail infants were less independent and spent more time with their mothers than the infants of bonnet females.

McKenna (1979) suggests that it might be more worthwhile to look at the relative needs of the mother and the infant at specific times, when it would be more

advantageous for one or the other to behave in such a way as to regulate the degree of proximity.

The present study exploits this suggestion and compares the behaviors of mothers and their infants when the females are in estrous to when they are not, assuming that it would be advantageous for the mother to remove herself from her infant at this time.

C. Summary

Although studies specifically addressing the subject of weaning are few, there are a number of research projects which cover mother-infant interactions during the onset and progression of weaning. A review of the literature concerning the mother-infant relationship in non-human primate clearly indicates that variability in the weaning-related behaviors of mothers and their infants exists both between and within species. Although the information regarding the factors contributing to this variation is inconsistent and confusing, there are some aspects of the mother-infant relationship which appear to be universal.

The present study will attempt to determine if this variability exists in the weaning-related behaviors of the mothers and their infants in a troop of semi free-ranging Japanese macaques and if the variability is related to the sociological, ontogenetic and ultimate factors discussed in this chapter. It should be possible to

make some general statements concerning the dynamics of the mother-infant interactions based on the results of this study.

II. Methods

A. Study Troop

Japanese macques (*Macaca fuscata*) are semi-terrestrial members of the family *Cercopithicidae*. They are indigenous to the Islands of Japan, ranging from 31 degrees to 41 degrees N latitude, which is the northern limit of non-human primates throughout the world (Tokuda 1961). They are classified as omnivorous, although their diet consists of nuts, buds, berries, shoots, leaves and bark (Fedigan 1982). The large multi-male, multi-female troops exhibit a kinship system which is articulated around the females resulting in "matrilineal kingroups which are closely associated with a small number of central adult males, usually unrelated" (Fedigan 1982:218).

Sexual behavior in Japanese monkeys is concentrated in a discrete breeding season which lasts 3 or 4 months. During this time the monthly reproductive cycles of the females include estrous cycles when the females are predisposed to mate. The gestation period varies between 150 to 170 days (Tokuda 1961).

The Arashiyama troop of Japanese macaques (*Macaca fuscata*) has been studied since the early 1950's giving them the distinction of being one of longest studied groups of monkeys living today (Wolfe 1979). Japanese primatologists initiated regular provisioning the facilitate observations, which resulted in a dramatic population increase and

eventually led to a fissioning into Arashiyama A and B troops in 1966 (Koyama 1970). Due to land constraints and encroaching human population in Japan, a troop consisting of 150 monkeys was relocated in South Texas near Laredo in February 1972 and renamed the Arashiyama West troop. Subsequently, in August 1981, the animals were moved to a large enclosure on a ranch near Dilley, South Texas.

The monkeys adapted well to their new environment and, although they are provisioned once daily with grain, corn, Purina Monkey Chow and range fodder (supplemented with peanuts and produce when available), they forage and feed on the local vegetation.

The study group, composed of almost 400 monkeys, is ideal for a behavioral study because the animals are almost free-ranging and exhibit a full range of interactions. They are readily accessible to the observer and are habituated to the presence of researchers. The availability of complete geneologies and life histories of the monkeys plus the tatoo system of identification, provide valuable assistance to the field researchers.

B. Study Site

The Arashiyama West Primate Centre is located on a 300,000 acre ranch near the town of Dilley, 60 miles south of San Antonio, Texas. The 50 acre enclosure is surrounded by an electrified fence which serves to deter most monkeys from leaving, even though peripheral males appear to be able to

come and go at will.

Although the surrounding brushland can be described as mesquite chapparal (Gouzoules 1980), the area inside the enclosure consists of two large fields bisected by a shallow ravine, in which there are two man-made ponds, and a road which serves as an access for the feeding truck. The vegetation inside the enclosure consists of a two-tiered canopy, predominantly *Acacia* (*Acacia* sp.) and mesquite (*Prosopis* sp.), surrounding the ravine and a ground cover of many indigenous grasses, wild flowers, and grain, which is planted annually. Deer towers, pallets and shed-like structures have been erected to provide shade and recreation for the monkeys.

South Texas supports a wide variety of wildlife, some of which are found inside the enclosure. Small animals, such as ground squirrels (*Spermophilus* sp), jack rabbits (*Lepus* sp.) and cottontails (*Sylvilagus* sp.) as well as several varieties of snakes, are frequently seen. The appearance of a rattlesnake (*Crotalus atrox*), which appears to be the only predator threatening the monkeys, provokes them to climb the nearest available trees and react with alarm calls. During the course of the present study, one adult male died from a rattlesnake bite.

C. Sample and Data Collection

This study was concerned with interactions between mothers and their current infants during the mating season. The data were collected using focal animal data sheets (Lehner 1979:124) to record the behaviors of the mothers (see Appendix 1). The focal animal sheets provided frequencies, durations, and sequences of behaviors, as well as information regarding the object and direction of interactions.

Sample

The subject animals consisted of 18 mothers chosen to control for the age, rank and parity of the mother as well as the sex and age of their infants. The 18 pairs (9 females with male infants and 9 females with female infants) were matched for the age of the infant within 2 weeks, the age of the mother and her rank (Table 1) Eleven out of eighteen subject females began their estrous cycles during the study.

Special mention must be made of female #71, who was one of the eleven estrous females who cycled during the study. Her data was included in the tests analyzing the variability in maternal weaning-related behaviors, the factors affecting the variability and the relationships between the maternal and infant weaning-related behaviors. However, since comparisons between the pre-estrous and estrous sessions were concerned with interactions between mothers and their infants (particularly maternal rejections), # 71 was

omitted from that series of tests because she was rarely with her infant while she was in estrus. Her infant spent only 15% of its time closer than 1 meter to her during the sessions when she was in estrus, compared to the average of 48% of the time the other infants spent closer than 1 meter to their mothers during estrous sessions.

Observation Procedures

The data were collected with the aid of a research assistant, from October to December, 1983, which coincided with the peak of the mating season. The infants ranged in age from 17 to 26 weeks at the beginning of the study which, according to the literature, is well into the weaning period (Gouzoules 1980). Having spent 3 weeks attending a field school at Arashiyama West Primate Centre in the spring of 1981, I was familiar with the research facility, the tattoo system of identification and focal animal procedures. Two weeks prior to actual data collection were devoted to acquainting myself and my research assistant with the subject animals and with as many other individuals as possible. Inter-observer reliability tests were conducted prior to data collection and subsequently during the study and an average consistency rate of 95% was achieved. A total of 486 hours in the field resulted in 344 hours of focal animal data taken in 30 minute sessions.

The sessions were conducted during 3 time periods daily to allow for the variations in the activity patterns of the

monkeys.

1. Three hours immediately after sunrise, when the animals were moving out of the trees to forage
2. Mid-day, or 4 to 7 hours after sunrise, when the animals were grooming and resting
3. Three hours before sunset, when the animal were foraging and returning to the trees for the night.

A 2 hour break was taken between the second and third periods to allow for provisioning, when interactions were the least natural.

One focal animal session was recorded on each female in each time period (a total of 54 sessions) before the next rotation was begun. This rotation was done systematically until some of the females began to cycle, at which time the major concentration was on estrus data.

Definitions

Estrus is described by Fedigan (1982:140) as:

female motivation (proceptivity) and/or willingness (receptivity) to mate.

Although the endocrine state of the females is not known, the present research is based on the assumption that estrus is "a discrete measurable behavioral and physical condition corresponding to-ovulation" (Fedigan 1982:140). Fedigan (1982:142) describes consort relationships as a "unique form of pair bonding in primates". In Japanese macaques, during mating season, a female will often form a consort bond or an exclusive relationship with a particular male, based on

sexual attraction. Although the bond is temporary, sometimes lasting only a few days, it is usually intense and frequently results in copulation (Fedigan 1982).

Daily scans were undertaken to assess the estrous state of the subject females. The following physical and behavioral characteristics were used to identify estrous females.

Physical Characteristics

1. Conspicuous redness of the perineal skin (Fedigan 1982:138)
2. Conspicuous redness of the facial skin (Fedigan 1982:138)
3. Bite wounds (Carpenter 1964)
4. Showing of blood in the vaginal area
5. Presence of coagulated seminal fluid in the vaginal area, commonly known as a "vaginal plug" (Carpenter 1964:310).

Behavioral Characteristics

1. Estrous hack (vocalization peculiar to estrous females)(Bullard 1984)
2. Changes in normal activity pattern, characterized by restlessness and irritability and movement away from the usual sub-group (Carpenter 1964)
3. Harrassed by males, as evidenced by heightened levels of chases, threats and bites by males (Fedigan 1982)
4. Consort or mating behavior with males or females.

Because these characteristics of estrus appeared over the course of several days, the females were not designated as "estrous" until the appearance of the vaginal plug and/or consort or mating behavior.

D. Data Collation

The data from the focal animal sheets were prepared for entry into the computer by recording the numerically coded information on 360 Assembler Coding Forms. Each line represented one behavior, while the columns represented sociological, contextual, durational and behavioral variables. The following units of the ethogram (see Appendix 2) were designated as weaning-related behaviors:

Mother

Break Contact, Nipple Withdrawal, Reject, Threatens Infant, Leave Infant, Wean Bite, Shake, Cuff, Pinch, Approach Infant, Grooms Infant.

Infant

Gecker, Tantrum, Nipple Contact, Lap, Sit Beside, Dorsal Carry, Ventral Carry, Follow Mother, Approach Mother, Leave Mother.

In order to test variables such as maternal rejections, infant distress reactions and attachment behaviors, which include a number of related behaviors, it was necessary to combine several ethogram units. This was done heuristically on the basis of similarity of purpose or function and the

following grouped variables were created:

MATERNAL REJECTION (TOTAL)-Leave Infant,
Break Contact, Nipple Withdrawal, Reject,
Threatens Infant, Wean Bite Pinch, Shake,
Cuff

MILD REJECTIONS-Leave Infant, Break Contact,
Nipple Withdrawal, Reject, Threatens Infant

PUNISH-Wean Bit, Pinch, Shake, Cuff

INFANT DISTRESS REACTIONS- Gecker, Tantrum

INFANT SEEKS MOTHER-Infant Follows, Approach
by Infant, Seek Nipple

INFANT/MOTHER CONTACT-Nipple Contact, Lap,
Sit Beside Mother, Ventral Carry, Dorsal
Carry, Mother Grooms Infant.

The six grouped variables will be distinguished from the single ethogram units by the use of upper case letters.

The duration of time the infants spent close to their mothers was important in a study concerning the mother-infant relationship therefore the variable "proximity" was used to define the duration of time the infants were closer than 1 meter to their mothers.

Because the study was concerned with an analysis of:

1. The overall variation of weaning-related behaviors with respect to sociological variables;
2. A comparison of weaning-related behaviors in estrous and non-estrous sessions; and
3. A determination of the variability of weaning-related

behaviors with respect to the increasing age of the infant over the course of the study, four separate data sets, created from the original data base, were used as the basis for statistical tests. These included the lumped behavioral variables, values which were adjusted to frequencies per session and durations which were calculated as percentages of the total duration of observations. All statistical tests were conducted using the Midas (Michigan Interactive Data Analysis System) computer program and the adjusted values.

E. Research Questions

In order to fulfill the objectives of the present research, the following questions were asked:

1. Are there appreciable individual differences in weaning-related behaviors of the mothers and their infants?

The mothers were compared for differences in the frequencies of MATERNAL REJECTION. The infants were compared for differences in the frequencies of INFANT DISTRESS REACTIONS and attachment measures, which included behavioral frequencies and the durations of MOTHER/INFANT CONTACT and proximity.

2. What sociological factors contribute to these behavioral differences?

The variation in the weaning-related behaviors of the mothers and their infants were analysed with respect to

the following factors: the rank, age, parity of the mother, the number of her immature offspring and the age and the sex of the infant.

3. Are the weaning-related behaviors of the mothers and their infants significantly different during the mothers' estrous periods?

Comparisons were made of the weaning-related behaviors of the mothers and their infants between:

- a. Pre-estrous and estrous sessions of the females who cycled
- b. The pre-estrous sessions of the females who cycled and the early sessions of the females who did not.
- c. The early and late sessions of the females who did not cycle. ²

4. What are the infants' responses to MATERNAL REJECTION?

The occurrence of MATERNAL REJECTION was tested for a relationship with the frequency of INFANT DISTRESS REACTIONS and the duration of MOTHER/INFANT CONTACT and proximity.

5. Which member of the mother/infant dyad is initiating the degree of proximity?

The proportions of infant and mother leaves to total leaves and infant and mother approaches to total

approaches was calculated for the overall study as well

²The females did not begin to cycle until late in the study period (on day 34 of the 57 day study), therefore the data collected on the females who did not come into estrous were divided into early (day 1 to 33) and late (day 34 to 57) sessions to control for the possibility that the time factor could contribute to behavioral variability.

as for estrous, non-estrous and consort sessions.

F. Data Analysis

Due to the small sample size and the potential for a non-normal distribution of the data, non parametric statistical tests were used in the data analysis (Lehner 1979). Differences between 2 groups were tested using the Mann-Whitney U test for two sample comparisons between independent samples and the Wilcoxon test for differences within the same sample. For variables with more than 2 groups such as maternal rank, the Kruskal-Wallis test statistic for multi-sample comparisons was used. The Kendall tau-b test and the Spearman rho correlation coefficient correlation statistics were used to test the association of variables of an analytical or continuous nature.

Data Set I

The data were analysed by mother and infant pairs. This provided:

1. Descriptive statistics to determine the range of variability in weaning-related behaviors
2. An overall analysis of weaning-related behaviors and durations of CONTACT and proximity with respect to the sociological variables described above.
3. Correlations of MATERNAL REJECTIONS to DISTRESS REACTIONS and ATTACHMENT behaviors of the infants
4. The proportion of infant leaves and approaches in

comparison to the leaves and approaches of the mother, as a measure of the degree of proximity.

Data Set II

The data on each of the females who cycled during the study were divided into pre-estrous, estrous and consort sessions. This division allowed for a comparison of weaning-related behaviors between different estrous states, rather than between mother-infant pairs. It also provided a comparison of weaning-related behaviors between the different estrous states of the 11 females who cycled during the study.

Data Set III

The weaning-related behaviors of the pre-estrous and estrous sessions of the females who cycled, and the early (day 1 to 33) and the late (day 34 to 57) sessions of the females who did not cycle were analysed. ³

This provided:

1. A comparison of the maternal and infant weaning-related behaviors over time of the females who did not cycle, testing for behavioral variability in early and late sessions when estrous was not a factor.
2. A comparison of the weaning-related behaviors of mothers and infants in the pre-estrous sessions of the females who cycled and the early sessions of the females who did not cycle, thereby testing for behavioral variability

³The data taken on the females who did not cycle were divided into early and late sessions to coincide, as far as possible, with the pre-estrous and estrous cycles of the females who did cycle.

before any of the study females began their estrous cycles.

Data Set IV

The data were analysed by the age of the infant, calculated in 2 week periods, which provided a measure of the relationships between the age of the infant as the study progressed and weaning-related behaviors.

III. Results

The infant Japanese macaques were spending almost one-half of the observed time closer than 1 meter to their mothers (49%), much of which was in actual physical contact with her (Table 2). During the afternoon hours, when the mothers were resting and grooming, the infants could be generally found on their mothers' nipple.

Since the observations were made during the daylight hours only,⁴ the total amount of time the infants spent with their mothers was considerably higher. Assuming that during the night, after the monkeys had returned to the trees to sleep, the infants would be in CONTACT or closer than 1 meter to their mothers most of the time, the average time in CONTACT and in close proximity to the mothers could approach (124/200) 62% and (149/200) 75% respectively.

A. Individual Variability in Weaning-Related Behaviors

Using the criterion of a high standard deviation relative to the mean (over one-half the value of the mean) as the measure of appreciable variability in the weaning-related behaviors of the mothers and their infants, it was determined that (Table 3):

1. There was appreciable variability in the weaning-related behaviors of the mothers (TOTAL REJECTS, MILD REJECTS, PUNISHES, mother approaches and mother leaves)
2. There was appreciable variability in the INFANT DISTRESS

⁴Data were collected from 7am to 7pm until daylight saving time ended and from 6am to 6pm thereafter.

REACTIONS and infant attempts to gain the nipple.

3. There was little variability in the frequencies of infant approaches, infant leaves and "INFANT SEEKS MOTHER"
4. There was little variability in the duration of time the infants spent in nipple contact, in CONTACT with their mothers and closer than 1 meter to their mothers.

The variability in weaning related behaviors, referred to in the literature, was only apparent in the behaviors of the mothers, and in INFANT DISTRESS REACTIONS and attempts at the nipple. The infants were leaving, approaching and SEEKING THEIR MOTHERS at much the same rate and consequently the time the infants spent in CONTACT and close to their mothers showed little variation.

B. Factors Affecting the Variability in Weaning-Related Behaviors

1. Sociological Factors

a. The Rank of the Mother (Tables 4-6)

The rank of the subject females was established from the records of the Arashiyama West Primate Centre which document the dominance structure of the troop. Comparisons of the weaning-related behaviors of the high, medium and low ranking mothers and their infants (N=6 of each) was made using the Kruskal-Wallis test.

There was no significant variation in the maternal weaning-related behaviors between the mothers of different dominance ranks. However infants of high ranking mothers approached and sought their mothers significantly more ($p=.0110$ $H=9.0263$ and $p=.0254$ $H=7.3421$ respectively), than infants of medium and low ranking mothers.

b. Parity (Tables 4-6)

The relationships between the number of infants born to each mother and the rates of weaning-related behaviors were tested using a Spearman rho correlation coefficient and Kendall tau-b test. There was a significant positive correlation between the number of infants born to the mothers and the rate of infant approaches ($p=.0011$ $\tau_b=.5797$ $r=.6875$) and "INFANT SEEKS MOTHER" ($p=.0076$ $\tau_b=.4764$ $r=.5976$). There was no significant relationship between the parity of the mother and the remaining weaning-related behaviors of the mothers and their infants.

c. The Age of the Mother (Tables 4-6)

The relationships between the age of the mother and the rates of weaning-related behaviors were tested using the Kendall tau-b test and the Spearman rho correlation coefficient. There was a significant positive relationship between the age of the mother and the rate of infant approaches ($p=.0256$ $\tau_b=.4100$ $r=.5500$) and a tendency for infants of older mothers to seek their mothers more ($p=.0903$

$\tau\text{-}b=.3107$ $r=.4469$). Obviously, the parity of the mother will be strongly related to her age. Using the Kendall $\tau\text{-}b$ test and the Spearman rho correlation coefficient, the relationship between these sociological variables was significant at $p<.001$ ($\tau\text{-}b=.7101$ $r=.8522$).

d. The Number of Immature Offspring (Tables 4-6)

Because young Japanese macaque females typically begin to cycle at 4 years of age and males mature sexually somewhat later, the number of immature offspring of each mother were calculated as the juveniles under 4 years of age. Since the maximum number of immature siblings was three, the mother infant dyads were divided into three groups, those having one, two and three immature siblings respectively.⁵ Using the Kruskal-Wallis test of the variability among the three groups, little difference was found between the weaning-related behaviors of the mothers and their infants with respect to the number of immature siblings.

e. The Sex of the Infant (Tables 4-6)

Comparisons of the weaning-related behaviors of mothers and their infants were made based on the sex of the infant using a Mann-Whitney U test. There were no significant differences between the weaning-related behaviors of the mothers and their female infants, and mothers and their male

⁵The group with no immature siblings consisted of only two females and was omitted from the tests.

infants.

2. Ontogenetic Factors

The relationship of the advancing age of the infant with the rates of maternal and infant weaning-related behaviors was tested using a Kendall tau-b test and a Spearman rho correlation coefficient (Table 7). It was found that:

1. There was no significant relationship between the advancing age of the infant and MATERNAL REJECTIONS and leaves.
2. The rate of INFANT DISTRESS REACTIONS was positively correlated to the advancing age of the infant ($p=.0095$ $\tau\text{-}b=.2260$ $r=.2972$).
3. The frequency with which the infant left its mother was negatively related to the advancing age of the infant ($p=.0467$ $\tau\text{-}b=-.1681$ $r=-.2387$).
4. The duration of the time the infants spent closer than 1 meter to their mothers was negatively related to the advancing age of the infant at a significance level of $p=.05$ ($p=.0373$ $\tau\text{-}b=-.1754$ $r=-.2554$).

Although the mothers did not reject their infants significantly more as they grew older, the infants reacted more and left their mothers less as the study progressed. The fact that the infants spent less time with their mothers as the study progressed is consistent with the results of other field studies.

3. Ultimate Factors

For the purpose of the following analyses, the subjects were divided into two groups, the females who cycled during the study and those who did not, Groups A and B respectively. In order to test the effect of time on the weaning-related behaviors of the females and their infants, Group A and B females were further subdivided as follows: ⁶

Group A1- Females who cycled, pre-estrous sessions (N=10)

Group A2- Females who cycled, estrous sessions (N=10)

Group B1- Females who did not cycle, sessions from day 1-33 (N=7)

Group B2- Females who did not cycle, sessions from day 34-57 (N=7).

The effect of the estrous state of the female on the weaning-related behaviors of the mothers and their infants was tested using a Mann-Whitney U test for comparisons between the females who cycled during the study and those who did not (Groups A and B), and a Wilcoxon test for comparisons within Groups A and B (Table 9).

1. Comparisons were made between the behavioral variables in pre-estrous and estrous sessions for 10 out of the 11 females who cycled during the study (Groups A1 and A2). The result was a significantly higher rate of MATERNAL REJECTIONS ($p=.0215$) in estrous sessions.

⁶Female #71 was omitted from the tests because she represented a deviant case, spending only 15% of her time during estrous sessions closer than 1 meter to her infant. The average duration of time spent closer than 1 meter to their infants was 48% for the other estrous females.

2. Since the females did not begin to cycle until late in the study period, on day 34 of the 57 day study, comparisons were made between the early (day 1 to 33) and the late (day 34 to 57) sessions of the females who did not cycle, to test for behavioral variability when the time period was the factor, not the estrous state of the female (Groups B1 and B2). The results of these comparisons indicated that there were no significant differences in the rates of any of the maternal or infant weaning-related behaviors, but that mothers tended to approach their infants more in the early sessions ($p=.0625$).
3. The behavioral variables in the pre-estrous sessions of the females who cycled and the early sessions of the females who did not cycle were compared in order to test for variability before the estrous cycles began (Groups A1 to B1). There were no significant differences in the weaning-related behaviors of the mothers and their infants between the pre-estrous sessions of the females who cycled and the early sessions of those who did not cycle.

When the MATERNAL REJECTIONS were partitioned into MILD REJECTIONS and PUNISHES, there was in all sessions a higher proportion of PUNISHES compared to MILD REJECTS (Table 10). Although the percentage of PUNISHES to MILD REJECTS was higher during estrous periods, this tendency was also present in the late sessions of the females who did not

cycle during the study, indicating a general tendency for the females to increase the severity of their maternal rejections over the 8 week study.

Given the influence of estrus demonstrated by these results, it was important to re-examine the significant results with respect to the sociological and ontogenetic variables by analysing the behaviors of Group A and B mothers and infants separately.

Sociological Factors– A Kruskal-Wallis test comparing the rate of infant approaches and INFANT SEEKS MOTHER across maternal ranks indicated that the infants of high ranking mothers in Group A approached their mothers significantly more than the other infants. However these behaviors did not vary significantly in the infants belonging to the females in Group B (Table 11). Thus, the significant variation in the initial test with the total sample is likely a reflection of differences in frequencies of infant approaches only for those females who cycled. A tendency for infants of high ranking females to approach mothers more was not present in both subgroups of the sample.

The relationships between the mothers' age and parity and the behavioral variables infant approaches and INFANT SEEKS MOTHER were investigated further (Table 11).

1. Using a Mann-Whitney U test for the comparisons between the females in Groups A and B, it was found that there was a tendency for the females who cycled to be older and have more infants ($p=.0882$ $U=26.00$ and $p=.0882$

$U=14.00$ respectively).

2. Using the Kendall tau-b test and the Spearman rho correlation coefficient to test for correlations between infants' approaches, and the mothers' age and parity in Groups A and B separately, the significant positive relationship between the rate of infant approaches and the mothers' age and parity was apparent for females in Group A but not for those in Group B.

The females who cycled tended to be the older and more experienced subject females, and their infants exhibited significantly more approach behaviors than the infants of the females who did not cycle.

Ontogenetic Factors— Using the Kendall tau-b test and the Spearman rho correlation coefficient, the relationships between the behavioral variables and the advancing age of the infants were investigated further by testing Groups A and B separately (Tables 7 and 8).

1. The positive relationship between INFANT DISTRESS REACTIONS and the advancing age of the infant was only significant in the infants of the females who cycled during the study ($p=.0213$ $\tau\text{-}b=.2559$ $r=.3265$).
2. The negative relationship of infant leaves and the advancing age of the infant was only significant in the infants of the females who did not cycle ($p=.0499$ $\tau\text{-}b=-.2827$ $r=-.3581$).
3. The negative relationship between proximity and the advancing age of the infant in the overall study

approached significance in the infants of the females who did not cycle ($p = .0942$ $\tau\text{-}b = -.2340$ $r = -.3202$), but not in the infants of the females who cycled.

4. There was a significant negative relationship between the advancing age of the infant and the duration of time the infants of Group B females spent in CONTACT with their mothers, that was not present in the overall sample or the infants of Group A females ($p = .0375$ $\tau\text{-}b = -.3190$ $r = -.3916$) (Table 8).
5. There was a tendency for the infants of Group A to approach their mothers less as they grew older ($p = .0860$ $\tau\text{-}b = -.1898$ $r = -.2558$) (Table 7). This tendency was not present in the Group B females or in the overall sample.

These results indicated that the relationships between the advancing age of the infants over the study period and several infant weaning-related measures were not the same for the Group A and B young.

C. Infant Reactions to Maternal Rejection

1. Infant Distress Reactions

The overall relationship of TOTAL REJECTIONS, MILD and PUNISHES, to INFANT DISTRESS REACTIONS was tested using Kendall $\tau\text{-}b$ test and the Spearman rho correlation coefficient (Table 12). Results indicated a significant positive relationship between INFANT DISTRESS REACTIONS, and TOTAL and MILD MATERNAL REJECTIONS ($p = .0210$ $\tau\text{-}b = .4040$

$r=.6212$ and $p=.0430$ $\tau\text{-}b=.3564$ $r=.5447$ respectively). There was a stronger positive relationship between INFANT DISTRESS REACTIONS and maternal PUNISHES ($p=.0057$ $\tau\text{-}b=.4753$ $r=.6739$). The rate of "mother leaves" was also positively related to INFANT DISTRESS REACTIONS at a .05 level of significance ($p=.0349$ $\tau\text{-}b=.3746$ $r=.4837$).

Although a major sequential analysis of the data was not undertaken, the question of behavioral sequences was pertinent to the discussion of INFANT DISTRESS REACTIONS to MATERNAL REJECTION. An analysis of the behaviors occurring before and after INFANT DISTRESS REACTIONS indicated that 54% were preceded by MATERNAL REJECTIONS (Table 13). Thirty-seven percent of infant geckers and tantrums were followed by nipple contact, while in 58% of the cases the infants were able to gain PHYSICAL CONTACT, including nipple contact, with their mothers (Table 14).

2. Infant Attachment Behaviors

The relationship between MATERNAL REJECTIONS and infant ATTACHMENT BEHAVIORS (infant approaches, INFANT SEEKS MOTHER and infant seeks the nipple) was tested using the Kendall $\tau\text{-}b$ test and the Spearman rho correlation coefficient (Table 12). There was a significant positive relationship between the rates of TOTAL and MILD REJECTIONS and the number of times the infants sought their mother's nipples ($p=.0418$ $\tau\text{-}b=.4281$ $r=.6440$ and $p=.0562$ $\tau\text{-}b=.3400$

$r=.4593$ respectively), while the positive relationship between PUNISHES and "infant seeks nipple" reached significance at the .01 level ($p=.0028$ tau- $b=.5238$ $r=.7411$).

An analysis of the behaviors occurring before and after "infant seeks nipple" (Tables 15 and 16) indicated that MATERNAL REJECTIONS accounted for 36% of the behaviors preceeding "infant seeks nipple" and 53% of those following the behavioral variable.

There was no significant relationship between the rates of TOTAL MATERNAL REJECTION, MILD or PUNISHES, and the duration of time the infants spent close to their mothers or in contact with them (Table 17).

D. The Respective Roles of Mothers and Their Infants in Maintaining Proximity

The infants were responsible for 84% of the total leaves and 97% of the total approach behaviors between mother and infant pairs (Tables 18 and 19). Although the percentage of "mother leaves" increased from 13% in pre-estrous sessions to 25% in estrous sessions, the same general tendency was apparent in a comparison of the proportion of "mother leaves" in the early and late sessions of the females who did not cycle (14% to 23% respectively). The highest proportion of "mother leaves" to the total leaves occurred when the estrous mother was in consort with another animal (33%).

The proportion of maternal approaches dropped slightly when the females came into estrous (3% in pre-estrous sessions to 1% in estrous sessions), while a comparison of the relative proportions between the early and late sessions of the females who did not cycle indicated a drop from 12% to 0% in maternal approaches. Because the rate of maternal approaches was so low in comparison to infant approaches, this tendency is not necessarily meaningful.

IV. Summary and Conclusions

A. Summary

1. Individual Variability in Weaning-Related Behaviors

The high standard deviation in relation to the mean frequencies in all the maternal behaviors established that there was an appreciable variability in the weaning-related behaviors of the 18 subjects (Table 3).

In contrast, the very low standard deviation relative to the mean rates of infant approaches, INFANT SEEKS MOTHER and infant leaves, and mean durations of the time the infants spent in nipple contact, BODY CONTACT and closer than 1 meter to their mothers, indicated little variability in these infant behaviors and measures of time spent with the mothers. The only meaningful variability in the infants' behaviors occurred in the rates of INFANT DISTRESS REACTIONS and attempts at nipple contact (Table 4). An analysis of the relationship between maternal and infant weaning-related behaviors indicated that INFANT DISTRESS REACTIONS and attempts at nipple contact were the only infant behaviors which were significantly correlated with any of the maternal weaning-related behaviors. The more the mothers REJECTED and left their infants, the more the infants' REACTED and sought the nipple (Table 12).

2. Factors Affecting Variability in Weaning-Related Behaviors

a. Sociological Factors

The variability in maternal weaning-related behaviors found between the 18 subjects in the present study did not appear to be affected significantly by any of the sociological factors often cited in the literature, such as the rank, age and parity of the mother, the number of her immature offspring, and the age and sex the infant (Table 4).

Although the variability in the rates of infant approaches and "INFANT SEEKS MOTHER" over the 18 infants was not appreciable, infants of high ranking mothers approached and SOUGHT THEIR MOTHERS significantly more than infants of medium and low ranking mothers. There was also a significant positive correlation between the mothers' age and parity ⁷ and the rate of infant approaches and "SEEKS MOTHER" (Table 5).

b. Ontogenetic Factors

There were no significant relationships between the increasing age of the infants and the maternal weaning-related behaviors, indicating that the mothers were not becoming more prone to REJECT their older infants (Table 7).

There was an overall positive relationship between the increasing age of the infant and the rate of INFANT DISTRESS

⁷The relationship between the mothers' parity and the rate of "infant SEEKS MOTHER" was only significant at the .10 level.

REACTIONS, while significant negative relationships were found between the advancing age of the infants and the rate of infant leaves and the duration of time they spent closer than 1 meter to their mothers (Table 8).

c. Ultimate Factors

The rate of MATERNAL REJECTION was significantly higher in the estrous sessions of the females in Group A (Table 9). This behavioral phenomenon was not evident in the comparison of the maternal weaning-related behaviors between the early and late sessions of the females in Group B or the the early sessions of the Group A and B females, when the estrous state of the mothers was not a factor (Table 9).

Although the infants of high ranking females in the overall sample approached their mothers significantly more than the other infants, this tendency was only significant in the infants of the high ranking mothers who cycled. It was established that there was a tendency for the females who cycled during this study to be the older and more experienced females in the sample. In separate tests run on the females who cycled during the study and those who did not (Table 11. Groups A and B respectively), ⁸ it was found that the positive relationship between the mothers' age and parity, and infant approaches was only apparent for the females in Group A. This relationship was not significant for the females in Group B.

⁸In the interests of clarity, the females who cycled will be referred to as Group A and the females who did not cycle as Group B for the remainder of the summary section.

The overall significant positive relationship between the increasing age of the infant and the rate of DISTRESS REACTIONS was only present in the infants of Group A females. At the same time, the overall negative relationships between the age of the infants and rate of infant leaves as well as the duration of time spent in the mothers' proximity were more apparent in the infants of the females of Group A (Tables 7 and 8).

3. The Dynamics of the Mother-Infant Interaction

a. Infant Reactions to Maternal Rejection

(1) Infant Distress Reactions

There was a significant positive relationship between INFANT DISTRESS REACTIONS and MATERNAL REJECTIONS, particularly with respect to PUNISHES (Table 12).

The analysis of behaviors occurring before and after INFANT DISTRESS REACTIONS indicated that in over half of the instances, MATERNAL REJECTION elicited geckers and tantrums. These DISTRESS REACTIONS were successful in reinstating or maintaining PHYSICAL CONTACT with the mother 58% of the time (Table 14).

(2) Infant Attachment Behaviors

There was a significant positive relationship between infants' attempts to seek the nipple and MATERNAL REJECTIONS, particularly PUNISHES. An analysis of the

behaviors preceding and following the infants' attempts to gain the nipple showed that, while over one-third of these attempts were preceded by MATERNAL REJECTION, in over half of the instances REJECTION was the mothers' response to the "infant seeks nipple" (Tables 15 and 16). An increase in maternal rejection did not result in any increase in the duration of the time the infants spent close to their mothers (Table 17).

b. The Respective Roles of the Mothers and Their Infants in Maintaining Proximity

The infants were responsible for the majority of the total leaves and approaches of the mothers and their infants, which would indicate that they were regulating the degree of proximity to their mothers (Tables 18 and 19).

B. Discussion

Weaning is an elusive process to research. In the present study, although it was obvious that the weaning process had begun, it was difficult to identify the degree of independence the young Japanese macaques had achieved, or the relative intensity of the MATERNAL REJECTIONS. Few studies have reported the actual duration of time the infants spend with their mothers between the ages of 4 to 8 months (Altmann 1980). The proportion of the time that the infants Japanese macaques in this study spent in actual CONTACT with their mothers (.24) approximates the average (30%) reported rhesus macaque infants in Cayo Santiago (Berman 1980). For the more slowly maturing baboons, Altmann (1980) and Nicolson (1982) noted that the average duration of time infants of this age spent in CONTACT with their mothers was somewhat higher, about 54% and 43% respectively. Perhaps an equally important finding of the present study was the significant decrease in the duration of time the infants spent closer than 1 meter to their mothers as they grew older (Table 8). These results are consistent with the findings of field studies on several species of non-human primates, for example Berman on rhesus macaques (1978), Altmann on yellow baboons (1980), Nicolson on olive baboons (1982), Itoigawa on Japanese macaques (1973) and Struhsaker on vervets (1971).

There is little in the literature on weaning which indicates the average rates of MATERNAL REJECTIONS for 4 to

8 month old macaque infants, or other non-human primate species, and therefore it is difficult to assess the relative intensity of the rejections in the mother-infant relationship in the present study. Hinde and Spencer-Booth (1967) calculated the ratio of MATERNAL REJECTIONS following nursing attempts in captive rhesus monkeys. They found a "temporary peak at around 20 weeks followed by a rise to about 0.5 at the end of the first year "(Hinde and Spencer Booth 1967:175). Because the ratio of MATERNAL REJECTION to nursing attempts in the present research on 4 to 8 month old Japanese macaque infants was 0.53 (Table 17), it would appear that the level of MATERNAL REJECTION in this case was at least as high as in captive rhesus macaques over the first year of the infants' life.

1. Individual Variability in Weaning-Related Behaviors

The marked variability in the weaning behaviors of the mothers, which had been observed in other field studies (Clark 1977; DeVore 1963; Nash 1978; Nicolson 1982), also was determined to be important in the present study. This degree of variability was not apparent in all the weaning behaviors of the infants, occurring only in the INFANT DISTRESS REACTIONS and attempts to gain the nipple. It was noteworthy that these were the only infant behaviors which were significantly correlated with the weaning behaviors of the mothers, suggesting that the variability in the infant behaviors can be predicted in the cases where the maternal

and infant behaviors are related.

In much of the research on the mother-infant relationship in macaque species (Berman 1980; Hinde 1974; Kaufman 1974) the duration of proximity and PHYSICAL CONTACT with the mother is used as a measure of infant independence. In the present study it was clear that there was very little variance in the degree of independence which had been achieved by the infants.

2. Factors Affecting Variability in Weaning-Related Behaviors

a. Sociological Factors

The variability in the maternal weaning-related behaviors was unexplained by the traditional sociological and ontogenetic factors. This was not entirely unexpected, given the lack of consistent evidence in the literature about the factors affecting behavioral variability in primate mothers and their 4 to 8 month old infants. Nicolson's (1982) research on weaning in olive baboons indicates a similar paucity of evidence in this area and she states that

the sources of variability in mother-infant relations and the development of independence remain unclear (1982:128).

Nash and Wheeler (1982) in an overview of the literature on the mother-infant relationship in non-human primates suggest that;

Mother's parity, rank and extremes of infant experience (as well as infant gender) have an

influence on the infant's behavior, but these factors may not account for all differences in the mother-infant interaction (1982:38),

but that there may be more "subtle qualitative differences (or "styles") in mother-infant pairs" (Nash and Wheeler 1982:39).

It is possible that some of the factors, particularly the mothers' age and parity, and the sex of the infant, were associated with behavioral differences in the mothers before the infants reached 4 months of age. Seay (1966) reports that multiparous and primiparous mothers generally show similar maternal behaviors but that the most common difference "appears to be a higher level of anxiety on the part of the primipera" (1966:164). This anxiety is more obvious in the early part of the mother-infant relationship. White and Hinde (1975) found a similar situation, in which the behavioral variability due to parity in rhesus macaque mothers and infants occurred in the early months of their study.

The sex of the infant was the sociological variable which showed the least variability in the weaning-related behaviors of the mothers or the infants. The frequencies of behaviors and durations of time the infants spent in CONTACT and near the mothers were extremely close for male and female infants. Again White and Hinde (1975) reported that the difference in MATERNAL REJECTION related to the sex of the infants were most marked between 12 to 18 weeks after birth, which was prior to the time-frame of the present

study.

Although many studies found that maternal rank did not affect the variability in weaning-related behaviors (Berman 1982; Nash 1978; Nicolson 1982), White and Hinde (1975) found that the differences in maternal behaviors related to the mother's rank were most obvious when the infants were between 6 to 14 weeks of age. Thus any variability in maternal behaviors due to rank could have been less obvious in 4 to 8 month old infants.

The infants of high ranking, older females with more offspring approached and sought their mothers more than the other infants. Since maternal age and parity are closely related variables, it is not surprising that they showed a relationship to the same behavioral variables. Nash and Wheeler state that

though the focus has so far been on the contrasts between primipares and multiparous females, differences between multiparous may also be important (1982:38).

Trivers (1974) suggests that the maternal behaviors of the female will change as they grow older since they have several infants and their infant-bearing years are numbered. It is possible that these females are more "tolerant" mothers (Nash and Wheeler 1982), which could explain the significant tendency for their infants to approach them more than infants of younger mothers.

In Gouzoules' study (1980), the infants of high ranking females were more dependent than the infants of the lower ranking females and were more likely to approach their

mothers. Since the literature suggests that high ranking females generally receive less aggression than lower ranking females (Nash and Wheeler 1982), it could be argued that infants of high ranking females approach their mothers more to benefit from the advantages of their mothers' status.

b. Ontogenetic Factors

It is important to note that the significant relationships between some of the behavioral variables and the increasing age of the infants over the duration of the study only held true for one of the two groups when the analyses were conducted on the infants of the females in Groups A and B separately (Table 7). The mothers in the overall study did not reject more or behave differently as their infants grew older; however the behaviors of the infants were affected if their mothers began to cycle in the latter part of the study. The fact that the significant relationship of INFANT DISTRESS REACTIONS to the increase in infant age was only apparent in infants of the females in Group A can probably be explained by the increased levels of MATERNAL REJECTION during estrous sessions. ⁹

The general tendency for non-human primate infants to spend less time in physical contact and close to their mothers as they grow older, which was more evident in the infants of Group B females, could have been retarded

⁹Table 11 indicated an overall significant positive relationship between MATERNAL REJECTIONS and INFANT DISTRESS REACTIONS.

somewhat by the estrous state of the Group A mothers. It is possible that the infants were more prone to remain close to their estrous mothers who were behaving in a manner unfamiliar to them.

c. Ultimate Factors

Gouzoules stated that, in the Arashiyama West troop of Japanese macaques,

The mothers of the infants do not become sexually active early in the mating season (1980:177).

This was certainly the case in the present research, as the females who cycled came into estrus during the last 3 weeks of the 8 week study.

A comparison of the maternal behaviors of the females in Group A, between pre-estrous sessions and estrous sessions, indicated that the rate of REJECTION was significantly higher during estrous sessions (Table 9). Since it could be argued that the increased rate of MATERNAL REJECTION was related to the fact that these occurred late in the study period, an attempt was made to control for the time factor by conducting the same analysis on the females of Group B. Comparisons of behaviors in the early and late sessions of these mothers indicated that, when estrous state was not a factor, there was no significant difference in the rate of MATERNAL REJECTION over the duration of the study. Further support for this result was evidenced by the fact that before the onset of estrus in Group A females, the variability in the rate of MATERNAL REJECTIONS was not

present in a comparison of the behaviors with those in the early sessions of of the Group B females.

These results show that the significantly higher level of MATERNAL REJECTION in the estrous sessions of the females of Group A was due to the estrous state of the female and not the time factor. It has also been established that MATERNAL REJECTIONS did not increase as the infants grew older which supports the position that the estrous state of the mothers appeared to be the one factor which could be used to predict variability in the rate of MATERNAL REJECTIONS. The heightened level of MATERNAL REJECTION during the estrous sessions of the females who cycled during the study substantiates quantitatively the observations of other field researchers (Horvat and Kraemer 1982; Jay 1963; Nash 1982; Ransom and Rowell 1972) who have documented a similar behavioral phenomenon. It also provides support for Trivers' theoretical position that the mother-infant conflict will be more severe when the female is predisposed to mate and produce another offspring.

Although the higher ranking, older and more experienced mothers appeared to be the focus of a higher rate of infant advances in the overall sample, the fact that these results were significantly more evident in the females who cycled indicates that behavioral differences in the infants were greater when the estrous state of the mother was a factor. A similar situation existed in the overall significant positive relationship between the increasing age of the

infants and the rate of INFANT DISTRESS REACTIONS, where the association was only present in the infants of the females who cycled.

Trivers (1974) not only provides a sociobiological explanation for the heightened level of maternal rejection during estrous sessions, he also stresses the fact that the offspring play an active role in the mother-infant conflict over weaning. He argues that, since the infants are smaller and less experienced, they can be expected to use psychological tactics to induce their mothers to provide more maternal care. The evidence that only the infants of the females who cycled displayed significantly more DISTRESS REACTIONS as they grew older, indicated that the estrous state of the mother contributed to the infants' behavioral strategies.

The fact that the infants of the mothers who cycled were approaching more in the case of high ranking, older and more experienced mothers and showing more DISTRESS REACTIONS as the infants grew older also could be interpreted to indicate that the infants were changing behaviorally to adapt to a new environment provided by the estrous mothers, as Galef (1981) suggests. While this is not overwhelming support for his theory, that behavioral changes in maturing mammals represent adaptations to new ecological niches, Galef admits that this effect will not be as obvious in non-human primates as it is in other mammals. In primates, where the periods of dependency are prolonged, socialization

as well as merely adapting to a new environment is more necessary for developing adult social behaviors.

3. The Dynamics of the Mother-Infant Interaction

a. Infant Reactions to Maternal Rejection

(1). Infant Distress Reactions

The relationship of INFANT DISTRESS REACTIONS to MATERNAL REJECTION (Table 12) in this study does not necessarily indicate that the rejections of the mother cause the infant DISTRESS REACTIONS. However a review of field studies on mother-infant relationship suggests that this is generally the case. For example, Altmann (1980:175) reports that

Maternal aggressive or punishing behavior was commonly followed by gestures or vocalizations of distress by the infant.

Nicolson (1982:117) found that

The distribution of acts of severe aggression mirrors the time course of the infant distress.

Their findings are corroborated in the present study by the stronger positive relationship between INFANT DISTRESS REACTIONS and maternal PUNISHES compared to MILD REJECTIONS.

The relationship of maternal leaves to INFANT DISTRESS REACTIONS is an extension of the same discussion, as maternal leaves were included as MILD REJECTIONS. The analysis of the immediate effects of INFANT DISTRESS REACTIONS indicated that, in over half the instances, the infants' geckers and tantrums resulted in the

reestablishment or maintainance of PHYSICAL CONTACT with their mothers.

(2). Infant Attachment Behaviors

In the overall weaning process, the infants gradually spend less and less time in close proximity and in CONTACT with their mothers. However, as discussed in Chapter 1, in some cases there is a temporary situation in which the MATERNAL REJECTION appears to be associated with heightened levels of attempts by the infants to be near their mothers. Hinde (1974), while stressing the importance of maternal rejection in the increasing level of separation between mothers and their infants, found a strong correlation between MATERNAL REJECTIONS and infants' attempts to be in CONTACT with their mothers.

Although my observations in the field would tend to support this conclusion, there did not appear to be any firm quantitative evidence for this behavioral phenomenon (Table 12). It is interesting to note that the level of MATERNAL REJECTION did not significantly affect the duration of time that the infants spent close to their mothers (Table 17). There was a significant positive relationship between infants' attempts to seek the nipple and MATERNAL REJECTIONS, particularly PUNISHES, but this was as much the result of the mothers responding to their infants' attempts to gain nipple CONTACT with rejection as the infants' reactions to MATERNAL REJECTION (Tables 15 and 16).

Because the significant effect of MATERNAL REJECTION on the infants' attachment behaviors has been reported in laboratory studies in various species of macaques (Harlow et al 1963; Hinde 1974 ; Kaufman 1974) and rarely in the field, it is possible this effect is intensified under laboratory conditions when the availability of social and environmental stimuli is limited.

• b. The Respective Roles of the Mothers and Their Infants in Maintaining Proximity

The strong indication that the infants were responsible for maintaining the degree of proximity to their mothers is consistent with other reports concerning the behavior of mothers and their infants after the onset of weaning. The percentage of all mother-infant approaches that were due to the infants minus the percentage of mother-infant leaves that were due to the infants (%Ap-%Lv in Tables 18 and 19) was used by Hinde and Spencer Booth (1967) and subsequently by Nash (1978)) to determine the member of the dyad assuming the primary role in maintaining proximity. When the results of %Ap-%Lv are negative, the mother is the responsible member and conversely, when the result is positive, the infant is the the maintainer of proximity. In the present study (Tables 18 and 19), the results of %Ap-%Lv (97%-84%) is plus 13, indicating that, at this stage, the infant is the primary instigator of proximity to its mother. In captive rhesus macaques the measure becomes positive at

about 5 months of age and remains over 10% thereafter (Hinde and Spencer Booth 1967). In feral baboons, the measure generally becomes positive between the infant ages of 5 and 6 months (Nicolson 1982). However, the fact that the infants are overtly instigating the degree of proximity to their mothers does not necessarily mean that the infants are actually determining the degree of independence which they are achieving.

Addressing the controversy referred to in Chapter 1 concerning the respective roles of the mothers and infants in the maintainance of proximity, one could argue for the role of either member of the dyad, depending on which researchers one quotes and the interpretation of the data. It would seem to be more productive to follow McKenna's (1979) suggestion and assess the mother-infant relationship in a specific situation.

Because the present study was partially concerned with a comparison of maternal and infant behaviors in estrous and non-estrous sessions, it was possible to view the relative roles of the mother and the infant during estrous and consort sessions when, presumably the mothers would be less likely to tolerate their infants' advances. The results indicate that the mothers in Group A were significantly more REJECTIVE during estrous sessions and that they left their infants proportionately more in estrous sessions and particularly in consort sessions, than they did in pre-estrous sessions (Table 18). Therefore it can be argued

that the mothers were more actively promoting the independence of their infants during the periods when they were motivated to mate, and actually consorting with a mate.

C. Conclusions

It is very easy for a researcher to lose contact with the insights gained in the field, in an effort to present a coherent statistical package based on a quantitative analysis of the data, so I would like to step back from the statistics for a moment and make some general statements founded on observations in the field.

It was clear that, although the infants were foraging for indigenous food and eating the food provided for them at the research centre, they were not really foraging and eating by themselves. Rather they were generally sitting close to their mothers during eating bouts. The time the infants were away from their mothers was usually spent interacting with their peers or investigating the environment. It was impossible to assess the amount of nutritional weaning which had been accomplished, or whether the infants would have been able to survive without their mothers' milk. Gouzoules (1982:172) states that in Japanese macaques;

Infants orphaned at 3 months of age have been known to survive and are capable of feeding themselves if they must.

However, in the present study, it appeared that the infants had not achieved a great degree of psychological independence at this stage.

The results of the present study indicated that the infants overwhelmingly controlled the degree of proximity to their mothers. In retrospect, the situation was not nearly

as clear as the results would suggest. A mother, foraging alone in the field, was almost certainly aware of her infant's whereabouts even when the young monkey was invisible to the observer. She would appear to be wandering aimlessly while gradually moving closer to her infant's play group. If her infant raced over to her, the action would be scored as "infant approaches mother" on the focal animal sheet, when in reality, the mother had made herself available to the infant. It appeared that many of the behaviors of the infant, which at first glance seemed to be random, were often the result of a subtle action on the part of the mother. The overall analysis of the data tends to reinforce these impressions.

The variability in maternal weaning behaviors described in the literature was evident in the Japanese macaque females in the present study. The individual variability appeared to be idiosyncratic insofar as it was unrelated to the sociological and ontogenetic variables tested. The estrous state of the mother appeared the one factor which could be used to predict variability in maternal rejection. Nicolson (1982:ii) reported that;

Weaning interactions usually preceded the resumption of the mother's sexual cycles by several months, and maternal reproductive condition was not, therefore a major determinant of the onset of rejection, in contrast to other field sites.

In the present study, the increased level of maternal rejection in the estrous sessions of the females who cycled showed that the estrous state of the mother was a factor in

the intensity of the weaning. Comparisons of maternal behaviors in the early and late sessions of the non-estrous females failed to reveal a similar escalation in weaning intensity. During estrous sessions, the mothers' interactive priorities were shifted from their infants to their sexual partners, therefore estrus may be a potent force in the facilitation of infant independence.

The pattern emerging from the results indicates that either the level of maternal rejection or the estrous state of the mother had a bearing on the variability in the infants' activities. Although there were no significant behavioral differences in the infants of the females who cycled when comparing estrous with pre-estrous sessions, they were showing different behavioral trends as they grew older when compared to the infants of the females who did not cycle. Clearly, in an intimate, interactive relationship such as the one a mother has with her infant, the behaviors of the one will have an effect on the behaviors of the other. The results of the present study could be interpreted to suggest that the variability in the weaning-related behaviors of the 4 to 8 month old infant Japanese macaques at Arashiyama West Primate Center was more a function of the variability in the behaviors and the activities of their mothers than a function of their own behavioral diversity.

I do not mean to imply that the infants were the passive recipients of their mothers actions, because it was clear that many of their behaviors were directed towards

receiving more maternal attention. Rather, it is my position that, although infants were displaying individuality in other aspects of their daily activities and social behaviors, they were not exhibiting variability in terms of their relationships with their mothers. The statistical results and field observations in the present study lead me to conclude that the mothers were exerting the major influence in the degree of independence exhibited by the young Japanese macaques. It is possible that, over the next 4 months, the infants' behaviors would have shown a much less obvious relationship to their mothers activities and a greater degree of individual variability.

Most of the research on infant ontogeny has been concentrated on defining general trends in the changes in the mother-infant relationship over time. It would be interesting to look at infant ontogeny from another perspective, the age at which infant non-human primates begin to exhibit behaviors which are not determined by maternal care.

V. Tables

Table 1 Study Sample

I.D. Number of the Female	Rank	Age	Parity	Number of Immature Offspring	Sex of the Infant	Infant Age in Weeks
34	Medium	17	7	2	Female	18
46	Medium	14	7	2	Male	21
49	High	17	9	3	Male	19
59	Low	12	4	1	Female	24
63	Low	12	4	1	Male	22
66	Medium	14	6	1	Female	24
71	Low	16	6	3	Female	22
72	Medium	14	9	3	Male	19
73	Low	12	5	2	Female	17
78	Low	9	2	1	Male	23
93	High	14	6	2	Male	26
122	High	14	8	2	Female	19
125	High	8	2	1	Female	21
126	High	15	7	1	Female	23
133	High	18	6	1	Male	24
161	Low	11	4	1	Male	24
212	Medium	6	1	0	Male	19
283	Medium	5	1	0	Female	20

Table 2 Duration of Infant Time Spent With Mothers

(All values are adjusted to the duration as a proportion of the total duration)

Animals	Nipple Contact	CONTACT	Proximity
34	.21	.27	.50
46	.12	.16	.35
49	.28	.32	.51
59	.10	.14	.38
63	.08	.14	.37
66	.10	.17	.44
71	.07	.14	.40
72	.12	.20	.49
73	.25	.38	.67
78	.14	.21	.47
93	.12	.19	.52
122	.18	.29	.49
125	.22	.30	.53
126	.24	.35	.62
133	.16	.23	.44
161	.19	.28	.61
212	.31	.37	.62
283	.16	.23	.46
Mean	.17	.24	.49
S.D.	.07033	.08046	.09203

Table 3 Descriptive Measures

(All values are adjusted to frequencies per session)
N=18

Variables	Minimum	Maximum	Mean	S.D.	
REJECTS	.14000	1.5300	.75333	.42476	X
MILD	.06000	.57000	.26944	.15880	X
PUNISH	.05000	1.23000	.48389	.33373	X
Mother Leaves	.02000	.36000	.14944	.09039	X
Mother Approach	0.	.16000	.02889	.03787	X
Infant Leaves	.57000	1.17000	.78056	.16104	0
Infant Approach	.47000	1.04000	.81499	.12226	0
INFANT SEEKS MO.	.47000	1.43000	1.0039	.21355	0
Seek Nipple	0.	.33000	.10611	.09763	X
INFANT DISTRESS REACTIONS	0.	.68000	.30500	.19713	X

X- Indicates appreciable variability

0- Indicates no appreciable variability

Table 4 Factors Affecting Maternal Weaning-Related Behaviors
(All values are adjusted to frequencies per session)
N=18

	Rank	Parity	Age of the Mother	# of Immature Offspring	Sex of the Infant
REJECTS	p= .7454 H= .58772	p= .3819 tau-b=.1663 r= .1943	p= .5177 tau-b=.1247 r= .1173	p= .3428 H=2.1411	p= .5000 U=35.000
MILD	p= .4046 H=1.8099	p= .7916 tau-b=.0621 r= .0851	p= .8199 tau-b=.0483 r= .0654	p= .8141 H= .4114	p= .5000 U=38.500
PUNISH	p= .5499 H=1.1959	p= .5957 tau-b=.1036 r= .2010	p= .8199 tau-b=.0483 r= .0665	p= .3331 H=2.1985	p= .5000 U=36.000
Mother Leaves	p= .6146 H=.97368	p= .4935 tau-b=.1407 r= .1417	p= .4454 tau-b=.1469 r= .1835	p= .7834 H= .48814	p= .6814 U=38.500
Mother Approach	p= .8988 H=.21345	p= .4562 tau-b=.1523 r= .2381	p= .5558 tau-b=.1218 r= .1525	p= .1135 H=4.3515	p= .6900 U=34.000

xxx Significant at p=.01 xx Significant at p=.05 Trend at p=.10

Table 5 Factors Affecting Infant Weaning Related Behaviors
(All values are adjusted to frequencies per session)
N=18

	Rank	Parity	Age of the Mother	# of Immature Offspring	Sex of the Infant
Infant Leaves	p = .1690 H = 3.5556	p = .7809 tau-b = .0588 r = .1050	p = .7324 tau-b = .0693 r = .1503	p = .6944 H = .72941	p = .5000 U = 27.000
Infant Approach	p = .0110 H = 9.0263 xxx	p = .0011 tau-b = .5797 xxx r = .6875	p = .0256 tau-b = .4100 xx r = .5500	p = .1654 H = 3.6103	p = .5000 U = 36.000
INFANT SEEKS MOTHER	p = .0254 H = 7.3241 xx	p = .0076 tau-b = .4764 xxx r = .5976	p = .0903 tau-b = .3107 x r = .4469	p = .5899 H = 1.0555	p = .5000 U = 36.500
Seek Nipple	p = .3738 H = 1.9678	p = .2359 tau-b = .2239 r = .2884	p = .4684 tau-b = .1339 r = .1648	p = .7956 H = .45726	p = .5000 U = 33.000
INFANT DISTRESS REACTIONS	p = .5899 H = 1.0556	p = .6767 tau-b = .0831 r = .1509	p = .7612 tau-b = .0623 r = .0817	p = .2635 H = 2.6673	p = .5000 U = 36.500

xxx Significant at p=.01 xx Significant at p=.05 x Trend at p=.10

Table 6 Factors Affecting the Duration of Infant Time Spent With Mothers
 (All values are adjusted to the durations as a proportion of the total duration)
 N=18

	Rank	Parity	Age of the Mother	# of Immature Offspring	Sex of the Infant
Nipple Contact	p= .2761 H=2.6404	p=1.0000 tau-b=-.0075 r=-.0183	p= .6751 tau-b=-.0840 r=-.1055	p= .7585 H=.55294	p= .3186 U=35.500
CONTACT	p= .2655 H=2.6520	p=1.0000 tau-b=-.0070 r=-.0094	p= .6477 tau-b=-.0963 r=-.1211	p= .8153 H=.50546	p= .3186 U=35.500
Proximity	p= .4495 H=1.5994	p= .1806 tau-b=-.0571 r=-.0564	p= .6477 tau-b=-.0963 r= .1807	p= .8153 H=.32904	p= .6814 U=37.500

xxx Significant at p=.01
 xx Significant at p=.05
 x Significant at p=.10

Table 7 Correlations of Weaning-Related Behaviors
with the Advancing Age of the Infants
 (All values are adjusted to frequencies per session)
 N=18

	Total Sample N=18	Group A N=11	Group B N=7
REJECTS	p= .3284 tau-b=-.0830 r=-.1117	p= .2909 tau-b=.1160 r= .1521	p= .9680 tau-b=.0088 r= .0066
MILD	p= .1032 tau-b=.1415 r= .1938	p= .2739 tau-b=.1245 r= .1663	p= .3539 tau-b=.1318 r= .1468
PUNISH	p= .7176 tau-b=.0313 r= .0351	p= .4706 tau-b=.0809 r= .1221	p= .4462 tau-b=-.1131 r= -.1609
Mother Leaves	p= .1165 tau-b=.1415 r= .1875	p= .2819 tau-b=.1263 r= .1636	p= .5498 tau-b=.0951 r= .1290
Mother Approach	p= .3648 tau-b=-.0884 r=-.1081	p= .4546 tau-b=-.0952 r=-.1061	p= .0765 tau-b=-.2911 x r=-.3196
Infant Leaves	p= .0476 tau-b=-.1681 xx r=-.2387	p= .3505 tau-b=-.1034 r=-.1299	p= .0499 tau-b=-.2827 xx r=-.3581
Infant Approach	p= .2935 tau-b=-.0896 r=-.1307	p= .0860 tau-b=-.1898 x r=-.2558	p= .9047 tau-b=.0202 r= .0116
INFANT SEEKS MO.	p= .9831 tau-b=-.0071 r=-.0009	p= .7684 tau-b=-.0336 r=-.0306	p= .6032 tau-b=-.0782 r=-.0812
Seek Nipple	p= .0831 tau-b=.1608 x r= .2048	p= .1189 tau-b=.1858 r= .2335	p= .8608 tau-b=.0322 r= .0433
INFANT DISTRESS REACTIONS	p= .0095 tau-b=.2260 xxx r=.2972	p= .0213 tau-b=.2559 xx r= .3265	p= .8622 tau-b=-.0301 r=-.0414

xxx Signif. at p=.01 xx Signif. at p=.01 x Trend at p=.10

Table 8 Correlations of the Durations of Infant Time
Spent With Mothers, and the Advancing Age
of the Infants

(All values are adjusted to the durations as a proportion
of the total durations)

	Total Sample N=18	Group A N=11	Group B N=7
Nipple Contact	p= .1076 tau-b=-.1364 r=-.1987	p= .3500 tau-b=-.1042 r= -.1582	p= .3268 tau-b=-.1438 r=-.1831
CONTACT	p= .1076 tau-b=-.1494 r=-.2061	p= .8158 tau-b=-.0281 r=-.0332	p= .0375 tau-b=-.3190 xx r=-.3916
Proximity	p= .0373 tau-b=-.1754 xx r=-.2554	p= .3721 tau-b=-.0987 r=-.1420	p= .0942 tau-b=-.2430 x r= -.3202

xxx Significant at $p=.01$

xx Significant at $p=.05$

x Trend at $p=.10$

Table 9 Variation in Weaning-Related Behaviors
Between Estrous and Non-Estrous Sessions
 (All values are adjusted to frequencies per session)

Comparisons between Pre-Estrous (A.1) and Estrous (A.2) sessions of the females who cycled (N=10), and the Early (B.1) and Late (B.2) sessions of the females who did not cycle (N=7).

	A.1 and A.2	B.1 and B.2	A.1 and B.1
Stat. Test	The Wilcoxon Test		The Mann-Whitney U Test
REJECTS	p= .0215 xx	p=1.0000	p= .5806 U=27.5000
MILD	p= .1094	p= .4531	p= .2862 U=26.500
PUNISH	p= .1094	p= .4531	p= .5806 U=29.000
Mother Leaves	p= .5078	p=1.0000	p= .1170 U=19.000
Mother approach	p= .3750	p= .0625 x	p= .3539 U=20.000
Infant Leaves	p= .7539	p= .4531	p= .3539 U=18.500
Infant Approach	p= .3438	p= .4531	p= .4149 U=30.000
INFANT SEEKS MO.	p= .7539	p=1.0000	p= .4194 U=31.000
Seek Nipple	p=1.0000	p=1.0000	p= .5806 U=30.500
INFANT DISTRESS REACTIONS	p= .3438	p= .6875	p= .1170 U=27.500

xxx Significant at p=.01

xx Significant at p=.05

x Trend at p=.10

Table 10 The Percentage of MILD REJECTIONS and PUNISHES
to the TOTAL REJECTIONS

	TOTAL	MILD	PUNISH	%MILD	%PUNISH
Overall	526	189	337	36%	64%
Pre-Estrous Sessions N=11	175	67	108	38%	62%
Estrous Sessions N=11	204	67	137	33%	67%
Consort Sessions N=11	58	18	40	31%	69%
Early Non- Estrous Sessions N=7	70	21	41	36%	64%
Late Non- Estrous sessions N=7	69	26	53	32%	68%

Table 11 Correlations of Maternal Rank, Age and Parity to Infant Approaches
and Infant SEEKS MOTHER
(All values are adjusted to frequencies per session)
N=18

	Rank		Age		Parity	
	A	B	A	B	A	B
Infant Approach	p= .0365 H=6.9148 xx	p= .3813 H=1.9286	p= .0184 tau-b=.6114 xx r=.7281	p= .2389 tau-b=.5270 r= .6483	p= .0274 tau-b=.5515 xx r=.6946	p= .1361 tau-b=.6000 r= .7091
INFANT SEEKS MOTHER	p= .0506 H=5.7633 x	p= .3813 H=1.9286	p= .3928 tau-b=.2282 r= .3272	p= .3813 tau-b=.4115 r= .5140	p= .1706 tau-b=.3651 r= .4932	p= .2389 tau-b=.4880 r= .5946

A-----Females who cycled
B-----Females who did not cycle

xxx Significant at p=.01
xx Significant at p=.05
x Trend at p=.10

Table 12 Correlations Between Maternal and Infant Behaviors
(All values are adjusted to frequencies per session)
N=18

	Infant Leaves	Infant Approach	Seek Nipple	SEEK MOTHER	INFANT DISTRESS REACTIONS
REJECTS	p = .1997 tau-b = -.2318 r = -.3821	p = .8804 tau-b = .0338 r = .0841	p = .0418 tau-b = .4281 xx r = .6440	p = .3479 tau-b = .1716 r = .3070	p = .0210 tau-b = .4040 xx r = .6262
MILD	p = .2754 tau-b = -.1980 r = -.2811	p = .6247 tau-b = .0943 r = .1697	p = .0562 tau-b = .3400 x r = .4593	p = .2594 tau-b = .2039 r = .3110	p = .0430 tau-b = .3564 xx r = .5447
PUNISH	p = .5743 tau-b = -.1056 r = -.2367	p = .5220 tau-b = .1212 r = .1977	p = .0028 tau-b = .5238 xxx r = .7411	p = .1306 tau-b = .2697 r = .3515	p = .0057 tau-b = .4753 xxx r = .6739
Mother Leaves	p = .2124 tau-b = -.2274 r = -.3537	p = .3248 tau-b = .1843 r = .2122	p = .0709 tau-b = .3176 x r = .4525	p = .1295 tau-b = .2734 r = .3515	p = .0349 tau-b = .3746 xx r = .4837
Mother Approach	p = .6423 tau-b = .0946 r = .1266	p = .9690 tau-b = .0140 r = .0059	p = .3921 tau-b = .1691 r = .2400	p = .7867 tau-b = .0560 r = .0872	p = .4379 tau-b = -.1529 r = -.1916

xxx Significant at p=.01 xx Significant at p=.05 Trend at p=.10

Table 13 Behaviors Preceding INFANT DISTRESS REACTIONS

Total DISTRESS REACTIONS=216
N=18

	Total	Percentage
REJECTIONS	124	57%
Seek nipple	13	6%
CONTACT	29	13%
Other	54	24%

Table 14 Behaviors Following INFANT DISTRESS REACTIONS

Total DISTRESS REACTIONS=216
N=18

	Total	Percentage
REJECTIONS	28	13%
Nipple Contact *	80	37%
CONTACT	126	58%
Other	40	19%

*Note-Because nipple contact is included in the CONTACT total, the total percentage is more than 100%.

Table 15 Behaviors Preceding Seek Nipple

Total Seek Nipple=75
N=18

	Total	Percentage
REJECTIONS	27	36%
Geckers	4	5%
Approach Mother	10	13%
CONTACT	18	24%
Other	16	22%

Table 16 Behaviors Following Seek Nipple

Total Seek Nipple=75
N=18

	Total	Percentage
REJECTIONS	40 *	53%
Geckers	17 *	23%
Nipple Contact	19	32%
Mother Groom	2	3%
Infant	5	7%
Other		

*Note-8 REJECTIONS and Geckers occurred simultaneously and were scored separately.

Table 17 Correlations Between MATERNAL REJECTIONS and the Durations of Infant Time Spent With Mothers

(All values are adjusted to frequencies per session)
N=18

	Nipple Contact	CONTACT	Proximity
REJECTS	p= .2738 tau-b=.2007 r= .2894	p= .3275 tau-b=.1800 r= .2693	p= .3472 tau-b=.1728 r= .3166
MILD	p= .4080 tau-b=.1533 r= .1916	p= .5736 tau-b=.1063 r= .1242	p= .4530 tau-b=.1391 r= .1334
PUNISH	p= .1988 tau-b=.2334 r= .3304	p= .1860 tau-b=.2392 r= .3199	p= .1301 tau-b=.2715 r= .4431

xxx Significant at $p=.01$

xx Significant at $p=.05$

x Trend at $p=.10$

Table 18 The Percentage of Infant and Mother Leaves
to Total Leaves

	Total	Infant	Mother	%Infant	%Mother
Overall	632	530	102	84%	16%
Pre-Estrous Sessions N=11	240	208	32	87%	13%
Estrous Sessions N=11	164	123	41	75%	25%
Consort Sessions N=11	46	31	15	67%	33%
Early Non- Estrous Sessions N=7	146	136	10	86%	14%
Late Non- Estrous Sessions N=7	69	53	16	77%	23%

Table 19 The Percentage of Infant and Mother Approaches
to Total Approaches

	Total	Infant	Mother	%Infant	%Mother
Overall	593	477	16	97%	3%
Pre-Estrous Sessions N=11	229	211	8	97%	3%
Estrous Sessions N=11	158	156	2	99%	1%
Consort Sessions N=11	48	46	2	93%	7%
Early Non- Estrous Sessions N=7	131	115	16	88%	12%
Late Non- Estrous Sessions N=7	75	75	0	100%	0%

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Appendix 1. Focal Animal Sheet

Subject: _____ Date: _____ Time: _____

Context: _____

Proximity: _____

TIME	ACTION	DIRECTION	OBJECT	COMMENTS

Appendix 2. Ethogram

¹⁰ States

These are ongoing behaviors which are recorded in terms of their occurrence and duration (Lehner 1979), and are arranged hierarchically and are mutually exclusive. The onset of time of each consecutive unit is recorded throughout the session.

1. Nipple contact- Infant in oral contact with mother's nipple(s).**
2. Lap- Infant sits in mother's lap.
3. Infant Sit Beside- Infant sits in bodily contact with its mother.**
4. Other Sit Beside- Other animal sits in bodily contact with the mother.**
5. Mother Grooms Infant- Mother brushes aside hair with one or both hands and carefully picks through the hair, carefully removing materials such as flakes of skin and parasites.**
6. Groom-direct- Subject grooms another animal.
7. Groom-receive- Subject is groomed.
8. Ventral Carry- Mother assists infant to her ventrum to be carried.*
9. Dorsal Carry- Infant supports itself on the dorsal surface of the mother, who is standing or moving.**
10. Infant Follows Mother- Infant travels directly behind

¹⁰Ethogram units after Fedigan (1974) are designated by * and units after Gouzoules (1980) are designated by **

and in the path of the mother.

11. Follow-direct- Subject follows another animal.
12. Follow-receive- Subject is followed by another animal.
13. Self Groom- Mother grooms herself.*
14. Flee- Mother moves away from a pursuing animal. May be walking or running.*
15. Chase-direct- Vigorous pursuit of other animal, accompanied by agonistic signals.*
16. Chase- receive.
17. Mount-direct- A complete mount involves clasping the ankles or calves of the partner with the feet and clutching its pelvis while performing a pelvic thrust. It is performed by both sexes or partner of either sex.
18. Mount-receive.**
19. Between mounts- Period of time between mounts.
20. Gecker- Infant emits "ik-ik-ik" vocalization.**
21. Weaning Tantrum- Convulsive jerks accompanied by a characteristic repeated vocalization(#20).**
22. Forage- To search for and eat native vegetation.**
23. Travel- Quadripedal locomotion.*
24. Fight- Two or more monkeys involved in striking and pushing each other. This is usually accompanied by screaming and loud vocalizations.*
25. Inactive- Animal sitting, lying down or sleeping. No activity being performed.*

Events

These are single or transitory actions which may be repeated consecutively and may be coincident with states.

26. Infant Approaches Mother- A direct advance of the infant towards its mother. Almost always a preliminary to social interaction.*
27. Mother Approaches Infant.
28. Approach-direct- Subject approaches another animal
29. Approach-receive- Subject is approached by another animal
30. Infant Leaves Mother- Infant breaks contact and moves more than a meter from her.**
31. Mother Leaves Infant- Mother breaks contact and moves more than a meter from her infant.**
32. Retrieve- Mother hurries to her infant in a stressful situation.*
33. Restrain- Mother prevents her infant from moving away from her. This is accomplished by holding a foot, hand or its tail.*
34. Seek Nipple- Infant attempts to fasten its mouth or hand on its mother's nipple.*
35. Break Contact- Mother physically separates herself from her infant.**
36. Nipple Withdrawal- Removal of nipple from the infant's mouth. Accomplished by either pushing the infant's head away or by raising the arms, putting the nipple out of

reach.**

37. Reject- Physically not allowing the infant to approach for contact or nursing, usually by pushing or turning away.**
38. Wean Bite- Special form of bite, in which the teeth are clamped slowly and obviously on the feet, hands or head of the fussing infant. There appears to be an unhappy but non-traumatic reaction of the infant, indicating that the pressure of the teeth is minimal.*
39. Pinch or Grab- To take hold of the infant's body by the hand and squeeze to the point of pain.*
40. Mother Threatens Infant- Facial expression directed towards the infant involving one or more of the following: hard stare, brow raised, ears back, mouth dropped open.*
41. Threat- direct- Subject threatens another animal.
42. Threat-receive- Subject is threatened by another animal.
43. Bite-direct- To seize another animal by the teeth.*
44. Bite-receive
45. Scream- A loud shrill vocalization.*
46. Estrous Hack- Vocalization given by females in estrus. This strongly resembles "gecker" (20).*
47. Fear Grimace- A submissive visual signal in which the lips are retracted from the teeth, with the teeth clenched.*
48. Lip Quiver-direct-A facial expression in which the head is tilted back slightly, the lips are pouted and moved

rapidly up and down.*

49. Displace-direct-One monkey approaches another and it moves away, usually from a resting place which the performer then occupies.*

50. Displace- receive

51. Shake- Violent manual shaking of the infant's body.*

52. Cuff- Mother hits her infant with the flat of her hand.*

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